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# Realignment of *Festuca* Subgenus *Schedonorus* with the Genus *Lolium* (Poaceae)

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**ABSTRACT.** Evidence from the literature of the close relationship of *Festuca* subg. *Schedonorus* to *Lolium* and its relatively distant relationship to *Festuca* subg. *Festuca* is briefly discussed. New combinations, *Lolium* subg. *Schedonorus*, *Lolium arundinaceum*, *Lolium giganteum*, *Lolium mazzettianum*, and *Lolium pratense*, are proposed to reconcile classification with known phylogeny.

The relationship between *Festuca* L. and *Lolium* L. (Poaceae) has long been an interesting classification problem. *Lolium* is readily distinguished from *Festuca* by its spicate inflorescence and lateral spikelets with a single glume. This morphology suggests the spikelike inflorescence structure in the tribe Triticeae Dumortier, where *Lolium*, in early treatments, was often placed. Nevaski (1934) was the first to place *Lolium* in the Poeae (= Festuceae) rather than the Triticeae. Information from diverse non-morphological sources, such as hybridization and cytology (e.g., Jenkin, 1959), oligosaccharides and water-soluble polysaccharides in caryopses (MacLeod & McCorquodale, 1958), endosperm structure (Tateoka, 1962), seed protein electrophoresis (Bułińska-Rodomska & Lester, 1988; Butkute & Konarev, 1982), serology (Butkute & Konarev, 1980, 1982; Fairbrothers & Johnson, 1961; Smith, 1969; Watson & Knox, 1976), chloroplast DNA (cpDNA) restriction endonuclease site patterns (Lehväslaiho et al., 1987; Soreng et al., 1990), cpDNA reassociation (Hilu & Johnson, 1991), and thermal denaturation of genomic DNA (King & Ingrouille, 1987), has supported the placement of *Lolium* in Poeae.

Spontaneous hybridization occurs commonly between species of *Festuca* subg. *Schedonorus* (P. Beauvois) Petermann and chasmogamous species of *Lolium*, particularly the type species of the genus, *L. perenne* L. (Barker & Stace, 1986; Humphries, 1980; Gymer & Whittington, 1973). Hybridization between *Lolium* and *Festuca* subg. *Festuca* rarely occurs spontaneously and is reported only for *Festuca rubra* L. (Stace, 1975). The latter is, however, also reported to hybridize with species in *Festuca*

subgenera *Festuca* and *Schedonorus* as well as *Vulpia* C. C. Gmelin (Ainscough et al., 1986; Knobloch, 1968; Saint-Yves 1929; Stace, 1975). Hybridization between *Festuca* (*Schedonorus*) *pratensis* Hudson and *Lolium perenne* (= *×Festulolium loliaceum* (Hudson) P. V. Fournier) was suspected as early as 1790 (see Jenkin, 1933). Reproductive barriers are not appreciably greater for this hybridization than for interspecific hybridization within *Festuca* subg. *Schedonorus* or between many species of *Lolium* (Jenkin, 1933; Stace, 1975). The degree of difficulty in producing artificial *L. perenne* × *F. pratensis* hybrids and the differential success of reciprocal crosses is similar to interspecific hybridization reported in various plant genera (e.g., Borrill et al., 1977; Gymer & Whittington, 1973). Extensive studies of artificial hybrids and their chromosome behavior (for references, see Jauhar, 1974, 1975; Terrell, 1966), as well as chromosome banding (Dawe, 1989; Thomas, 1981), have indicated the homology of chromosomes and their genetic compatibility. In auto-allotriploids and amphidiploids of *L. perenne*, *L. multiflorum* L., and *F. pratensis*, synapsis of homeologous chromosomes usually occurs as multivalents or even bivalents, in spite of the presence of true homologues (Jauhar, 1974, 1975). Diploid crosses of these taxa show high bivalent formation (87–100%) with 0.783–0.896 chiasmata per chromosome pair (Jauhar, 1975). Such observations have led many taxonomists and cytogeneticists to suggest that *Festuca* and *Lolium* could be combined, in whole (e.g., Jauhar, 1975; Knobloch, 1963; Löve, 1963; Stebbins, 1956; Terrell, 1966; Ullmann, 1936) or in part (e.g., Tutin, 1956).

Amalgamation of *Festuca* and *Lolium* has been proposed as early as 1898 (M'Alpine, 1898), but no valid combinations of *Festuca* subg. *Schedonorus* taxa within *Lolium* are available. Raspail (1829), however, included *F. pratensis* (under the name *F. elatior* L.) and *F. loliaceum* Hudson (= *F. pratensis* × *L. perenne*) in his examination of *Lolium* as *L. festuca* Raspail and *L. festucoides* Raspail, respectively. Proposed on the basis of morphological and ecological continua observed between these taxa and

species of *Lolium*, Raspail considered this classification physiological rather than taxonomic. Such continua would be expected between hybridizing taxa and their derivatives. Gross morphology and cytological differences between *Festuca* and *Lolium* have been cited as reasons for not combining the genera (Clayton & Renvoize, 1986; Jenkin, 1933; Malik & Thomas, 1966; Raspail, 1829; Terrell, 1968).

Jenkin (1933) acknowledged the close phylogenetic relationship between *Lolium* and *Festuca* subg. *Schedonorus* and the relatively distant relationship of these taxa to *Festuca* subg. *Festuca*. He did not feel, however, that their classification was incumbent on evolutionary relationships. Bulińska-Rodomska & Lester (1988) detected similar relationships in a phenetic analysis of 50 morphological characters when they excluded six that were associated with the spicate inflorescence of *Lolium*. Their principal components analysis identified 11 characters in the first factor axis that separated the two lineages with the exception of *Vulpia alopecuros* (Schousboe) Dumortier. The latter taxon grouped with *Lolium* and *Festuca* subg. *Schedonorus* in the first axis but was clearly separated in the second axis. *Lolium* and *Festuca* subg. *Schedonorus* were not separated by either of the first two components.

Analysis of cpDNA restriction site variation (Darbyshire & Warwick, 1992; Lehväslaiho et al., 1987), chromosome synaptic ability (Jauhar, 1975), seed protein electrophoresis (Bulińska-Rodomska & Lester, 1988), and certain morphological data sets (Bulińska-Rodomska & Lester, 1988; Stebbins, 1956) suggests congeneric status for *Lolium* and *Festuca* subg. *Schedonorus* as a lineage distinct from species of *Festuca* subg. *Festuca*. This is consistent with other nonmorphological studies (Butkute & Konarev, 1980, 1982; Hilu & Johnson, 1991; King & Ingrouille, 1987; MacLeod & McCorquodale, 1958; Smith, 1969; Watson & Knox, 1976). The polyphyletic nature of *Festuca* sensu lato and its relationship to *Lolium* have not always been appreciated in these latter studies, because, for practical reasons, species of *Festuca* subg. *Schedonorus* are frequently used as the sole representatives of the large and diverse genus *Festuca*.

Polyphyly in *Festuca* has been considerably reduced since the concept of Linnaeus. Several groups (including *Vulpia* (Clayton & Renvoize, 1986) and *Hellerochloa* Rauschert (Tzvelev, 1989)), more closely related to *Festuca* subg. *Festuca* than *Festuca* subg. *Schedonorus*, are recognized as separate genera in some recent treatments. Consistent with some morphological interpretations (e.g., Macfarlane & Watson, 1982), cpDNA restriction site data

of North American species (Darbyshire & Warwick, 1992) indicate that *Leucopoa* Grisebach (excluding *Festuca* subg. *Leucopoa* sect. *Breviaristatae* Kri-votulenko) is also more distantly related to *Festuca* subg. *Festuca* than some of these taxa and should be recognized at the generic level. Inclusion of *Leucopoa* sect. *Leucopoa* in *Festuca* would require the inclusion of *Festuca* subg. *Schedonorus*, *Vulpia*, and *Lolium* for *Festuca* to be monophyletic.

The recognition of *Schedonorus* as a distinct genus seems unwarranted. Excluding the overemphasized inflorescence characters, it is hardly distinguishable from *Lolium* in morphology (Bulińska-Rodomska & Lester, 1988). The symmetrical chromosomes and limited polyploidy in the genus *Lolium* are plesiomorphic character states and cannot be used to define a monophyletic clade. Furthermore, the derived conditions of polyploidy and asymmetrical chromosomes found in *Schedonorus* and other subgenera of *Festuca* are highly homoplastic in grasses and are not irreversible. The reduction of the inflorescence from a panicle to a spike, with concomitant modifications to other reproductive structures, is the only derived morphological or cytological feature uniting species of *Lolium* and distinguishing them from their closest relatives. The trend from panicle to spike or raceme is homoplastic in other taxa of the Poeae and may not be synapomorphic in *Lolium*. Additionally, cpDNA restriction site data indicate less divergence of this genome between *L. perenne* and species of *Festuca* subg. *Schedonorus* than between some members of the *Festuca ovina* L. complex of *Festuca* subg. *Festuca* (Darbyshire & Warwick, 1992).

The accommodation of *Festuca* subg. *Schedonorus* in *Lolium* would require only slight change to published generic descriptions. Several morphological features of *Festuca* subg. *Schedonorus* are consistent with its classification in *Lolium*. Shared characters include wide, flat leaf blades with fascicles of sclerenchyma opposite the veins or forming girders between the epidermes at the major veins (plesiomorphic), entirely glabrous ovary apices (homoplastic in *Festuca* and *Lolium*), caryopses adhering to the paleas (synapomorphic in *Lolium/Schedonorus*, versus free in *Festuca*), subterminal style insertion (synapomorphic in *Schedonorus/Lolium*), and falcate leaf blade auricles (synapomorphic in *Schedonorus/Lolium*, which are not found in any related group).

The Old World taxa, *Festuca* subg. *Montanae* (Hackel) Nyman and *Festuca* sect. *Scariosae* Hackel, are known to be more closely related to *Festuca* subg. *Schedonorus* than *Festuca* subg. *Festuca*. At

least some of the species in these taxa may prove to belong to the clade including *Lolium* and *Festuca* subg. *Schedonorus* as has been suggested by cytological studies (Borrill et al., 1977; Chandrasekharan & Thomas, 1971). The phylogeny is complicated by the apparent allopoloids, between diploids of *Festuca* subg. *Schedonorus* and *Festuca* sect. *Scariosae*, seen in polyploid members of the *Festuca arundinacea* Schreber complex in northwest Africa (Borrill, 1972). Failure of meiotic chromosome pairing (1.20 bivalents per cell) in crosses between diploids of *Festuca* subg. *Schedonorus* (*F. pratensis*) and *Festuca* subg. *Montanae* (*F. drymeja* F. K. Mertens & W. D. J. Koch) has been attributed to differences in chromosome size (Morgan et al., 1986). Even lower pairing frequency is observed between diploids of *Festuca* subg. *Schedonorus* (*F. pratensis*) and *Festuca* subg. *Festuca* (*F. polesica* Zapalowicz), although there is much less of a difference in chromosome size (Morgan et al., 1986). If the relationships of *Festuca* subg. *Montanae* and *Festuca* sect. *Scariosae* are with the *Lolium/Schedonorus* rather than the *Festuca* sensu stricto lineage, this will not solve the questions as to whether *Lolium* should be united with, or *Schedonorus* separated from, *Festuca*. Further work may indicate a need to transfer species of *Festuca* subg. *Montanae* and *Festuca* sect. *Scariosae* to *Lolium* or at least to remove them from *Festuca*.

The paniculate inflorescence and the presence of the lower glume are the principal morphological characteristics separating *Festuca* subg. *Schedonorus* from *Lolium* and connecting the former taxon with *Festuca*. These serve as subgeneric characters in the treatment proposed here. Transferring the four species of *Festuca* subg. *Schedonorus* to *Lolium* is a much more practical solution to the obvious difficulties of combining the nomenclature of these two complex Linnaean genera under the caveat of monophyletic classification.

The name *Festuca elatior* L. was lectotypified by Linder (1986), and, although it has priority over *F. arundinacea* Schreber, has been proposed as a *nomina rejicienda* under ICBN Art. 69 by Reveal et al. (1991). The present usage (*F. arundinacea*) is followed here to avoid nomenclatural confusion.

**Lolium** subg. **Schedonorus** (P. Beauvois) S. J. Darbyshire, comb. nov. Basionym: *Schedonorus* P. Beauvois, Ess. Agrostogr.: 99, 177. 1812. *Festuca* sect. *Schedonorus* (P. Beauvois) W. D. J. Koch, Syn. Fl. Germ. Helv.: 813. 1837. *Festuca* subg. *Schedonorus* (P. Beauvois) Petermann, Deutschl. Fl.: 643. 1849.

TYPE: *F. elatior* L. (= *F. arundinacea* Schreber) (lectotype, selected by Niles & Chase (1925)).

**Lolium arundinaceum** (Schreber) S. J. Darbyshire, comb. nov. Basionym: *Festuca arundinacea* Schreber, Spic. Fl. Lips.: 57. 1771. *Bromus arundinaceus* (Schreber) A. W. Roth, Tent. Fl. Germ. 2: 141. 1789. *Schedonorus arundinaceus* (Schreber) Dumortier, Observ. Gramin. Belg.: 106. 1824. *Festuca elatior* var. *arundinacea* (Schreber) C. F. H. Wimmer, Fl. Schles. Ed. 3: 59. 1857. *Festuca elatior* subsp. *arundinacea* (Schreber) Čelakovský, Prodr. F. Böhmen 1: 51. 1867. TYPE: Scheuchzer, *Agrostographia*, tab. V, fig. 18. 1719 (lectotype, selected by Reveal et al. (1991)).

**Lolium giganteum** (L.) S. J. Darbyshire, comb. nov. Basionym: *Bromus giganteus* L., Sp. Pl.: 77. 1753. *Festuca gigantea* (L.) Villars, Hist. Pl. Dauph. 2: 110. 1787. *Avena gigantea* (L.) R. A. Salisbury, Prodr. Stirp. Chap. Allerton: 23. 1796. *Schedonorus giganteus* (L.) Gaudin ex J. J. Roemer & J. A. Schultes, Syst. Veg. 2: 644. 1817, as "Schenodorus giganteus" pro syn. *Bromus giganteus* L. *Bucetum giganteum* (L.) Parnell, Grass. Scotland: 108, pl. 47. 1842. *Zerna gigantea* (L.) Panzer ex B. D. Jackson, Index Kew. 2: 1249. 1895. *Forasaccus giganteus* (L.) Bubani, Fl. Pyren. 4: 383. 1901. TYPE: Europae sylvis siccis.

Roemer and Schultes published the name *Lolium giganteum* (Syst. Veg. 2: 750. 1817.) as a synonym of *L. maximum* Willdenow. This name has sometimes been cited *Lolium giganteum* hort. ex Roemer & Schultes as a synonym of *L. temulentum* L. (e.g., Terrell, 1968). According to ICBN Art. 34.1 this name is not validly published and thus the epithet, *giganteum*, is available for the proposed combination.

**Lolium mazzettianum** (E. B. Alexeev) S. J. Darbyshire, comb. nov. Basionym: *Festuca mazzettiana* E. B. Alexeev, Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 82(3): 99. 1977, nom. nov. pro *Festuca mairei* Hackel ex Handel-Mazzetti, Symb. Sin. 7: 1288. 1936, non Saint-Yves 1922. TYPE: China. Yunnan: talus des Uzuru, 3 June 1908, Ducloux 867 (lectotype, selected by Alexeev (1977), W).

**Lolium pratense** (Hudson) S. J. Darbyshire, comb. nov. Basionym: *Festuca pratensis* Hudson, Fl. Angl.: 37. 1762. *Festuca fluitans* var. *pratensis* (Hudson) Hudson, Fl. Angl. Ed. 2: 47. 1778. *Schedonorus pratensis* (Hudson) P. Beauvois, Ess. Agrostogr.: 99, 163, 177. 1812. *Bromus pratensis* (Hudson) K. P. J. Sprengel, Syst. Veg. 1: 359. 1825, non Lamarck 1785. *Lolium festuca* Raspail in Saigey & Raspail, Ann. Sci. Observ. 2: 244. 1829, comb. inval. *Lolium festuca* Raspail ex Mutel, Fl. Franç. 4: 111. 1837, pro syn. *Festuca pratensis* Hudson. *Bucetum pratense* (Hudson) Parnell, Grass. Scotland: 105, pl. 46. 1842. *Festuca elatior* var. *pratensis* (Hudson) A. Gray, Manual Ed. 5: 634. 1867. *Festuca elatior* subsp. *pratensis* (Hudson) Hackel, Bot. Centralbl. 8: 407. 1881. *Tragus pratensis* (Hudson) Panzer ex B. D. Jackson, Index Kew. 2: 1099. 1895. TYPE: Herb. Sloane 125.16 (BM-SL) (lectotype, selected by Reveal et al. (1991)).

**Lolium ×festucaceum** Link, Linnaea 2: 235. 1827. *Festuca loliacea* Hudson, Fl. Angl.: 38. 1762. *Festuca fluitans* var. *loliacea* (Hudson) Hudson, Fl. Angl. Ed. 2: 47. 1778. *Poa loliacea* (Hudson) Koeler, Descr. Gram.: 207. 1802. *Schedonorus loliaceus* (Hudson) P. Beauvois, Ess. Agrostogr.: 99, 163, 177. 1812. *Festuca pratensis* var. *loliacea* (Hudson) Saint-Amans, Fl. Agen.: 42. 1821. *Brachypodium loliaceum* Link, Hort. Berol. 1: 42. 1827, comb. inval. *Lolium festucoides* Raspail in Saigey & Raspail, Ann. Sci. Observ. 2: 243. 1829, comb. inval. *Festuca fluitans* Leers ex Kunth, Enum. Pl. 1: 405. 1833, non L. 1753, pro syn. *Festuca loliacea* Hudson. *Lolium festucoides* Raspail ex Mutel, Fl. Franç. 4: 112. 1837, pro syn. *Festuca loliacea* Hudson. *Glyceria loliacea* (Hudson) Godron, Fl. Lorraine 3: 168. 1844. *Tragus loliaceus* (Hudson) Panzer ex B. D. Jackson, Index Kew. 2: 1099. 1895. ×*Festulolium loliaceum* (Hudson) P. V. Fournier, Quatre Fl. France: 81. 1935. TYPE: England. London: near Vauxhall, ad vias et in pascuis sed rarius.

The “intergeneric” hybrid ×*Festulolium loliaceum* is deemed a hybrid of congeneric taxa under the classification proposed here. The correct name under this scheme is *Lolium ×festucaceum* Link.

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#### Literature Cited

- Ainscough, M. M., C. M. Barker & C. A. Stace. 1986. Natural hybrids between *Festuca* and species of *Vulpia* section *Vulpia*. Watsonia 16: 143–151.
- Alexeev, E. B. 1977. To the systematics of Asian fescues (*Festuca*). I. Subgenera *Drymanthele*, *Subulatae*, *Schedonorus*, *Leucopoa*. Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 82(3): 95–102. [In Russian.]
- Barker, C. M. & C. M. Stace. 1986. Hybridization in the genera *Vulpia* and *Festuca*: Meiotic behaviour of artificial hybrids. Nordic J. Bot. 6: 1–10.
- Borrill, M. 1972. Studies in *Festuca*. III. The contribution of *F. scariosa* to the evolution of polyploids in sections *Bovinae* and *Scariosae*. New Phytol. 71: 523–532.
- \_\_\_\_\_, M. Kirby & G. Morgan. 1977. Studies in *Festuca*. 11. Interrelationships of some putative diploid ancestors of the polyploid broad-leaved fescues. New Phytol. 78: 661–674.
- Bulińska-Rodomska, Z. & R. N. Lester. 1988. Intergeneric relationships of *Lolium*, *Festuca*, and *Vulpia* (Poaceae) and their phylogeny. Pl. Syst. Evol. 159: 217–227.
- Butkute, B. L. & A. V. Konarev. 1980. An immunological study of the seed proteins of the rye-grass in connection with the phylogeny of the genus *Lolium*. Bot. Zhurn. (Moscow & Leningrad) 65: 1453–1458. [In Russian.]
- \_\_\_\_\_, & \_\_\_\_\_. 1982. Studies of the seed proteins in the genera *Lolium* and *Festuca* (Poaceae) in connection with their phylogeny. Bot. Zhurn. (Moscow & Leningrad) 67: 812–819. [In Russian.]
- Chandrasekharan, P. & H. Thomas. 1971. Studies in *Festuca*. 6. Chromosome relationships between *Bovinae* and *Scariosae*. Z. Pflanzenzücht. 66: 76–86.
- Clayton, W. D. & S. A. Renvoize. 1986. Genera Gramineum. Grasses of the World. Kew Bull., Addit. Ser. 13: 1–389.
- Darbyshire, S. J. & S. I. Warwick. 1992 [1993]. Phylogeny of North American *Festuca* (Poaceae) and related genera using chloroplast DNA restriction site variation. Canad. J. Bot. 70: 2415–2429.
- Dawe, J. C. 1989. Sectional survey of Giemsa C-banded karyotypes in *Festuca* L. (Poaceae: Festuceae): Systematic and evolutionary implications. Thesis, University of Vienna.
- Fairbrothers, D. E. & M. A. Johnson. 1961. The precipitin reaction as an indicator of relationship in some grasses. Recent Advances in Botany 1: 116–120.
- Gymer, P. T. & W. J. Whittington. 1973. Hybrids between *Lolium perenne* L. and *Festuca pratensis* Huds. New Phytol. 72: 411–424.
- Hilu, K. W. & J. L. Johnson. 1991. Chloroplast DNA reassociation and grass phylogeny. Pl. Syst. Evol. 176: 21–31.
- Humphries, C. J. 1980. *Lolium* L. Pp. 153–154 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (editors), Flora Europaea, Vol. 5. Cambridge Univ. Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney.
- Jauhar, P. P. 1974. Chromosome pairing in some triploid and trispecific hybrids in *Lolium*–*Festuca* and its phylogenetic implications. Chromosomes Today 5: 165–177.

- . 1975. Chromosome relationships between *Lolium* and *Festuca* (Gramineae). *Chromosoma* 52: 103–121.
- Jenkin, T. J. 1933. Interspecific and intergeneric hybrids in herbage grasses. Initial crosses. *J. Genet.* 28: 205–264.
- . 1959. Fescue species (*Festuca* L.). Pp. 418–434 in H. Kappert & W. Rudorf (editors), *Manual of Plant Breeding*, Vol. 4. Paul Parey, Berlin.
- King, G. J. & M. J. Ingrouille. 1987. Genome heterogeneity and classification of the Poaceae. *New Phytol.* 107: 633–644.
- Knobloch, I. W. 1963. The extent of hybridization in the Gramineae. *Darwiniana* 12: 624–628.
- . 1968. A check list of crosses in the Gramineae. East Lansing, Michigan.
- Lehväslaiho, H., A. Saura & J. Lokki. 1987. Chloroplast DNA variation in the grass tribe Festuceae. *Theor. Appl. Genet.* 74: 298–302.
- Linder, H. P. 1986. Diverse notes on southern African Pooids. *Bothalia* 16: 59–61.
- Löve, A. 1963. Cytotaxonomy and generic delimitation. *Regnum Veg.* 27: 45–51.
- MacLeod, A. M. & H. McCorquodale. 1958. Water-soluble carbohydrates of seeds of the Gramineae. *New Phytol.* 57: 168–182.
- Macfarlane, T. D. & L. Watson. 1982. The classification of Poaceae subfamily Pooideae. *Taxon* 31: 178–203.
- M'Alpine, A. N. 1898. Production of new types of forage plants—Clovers and grasses. *Trans. Highland and Agric. Soc. Scotland*, Ser. 5, 10: 135–165.
- Malik, C. P. & P. T. Thomas. 1966. Karyotypic studies in some *Lolium* and *Festuca* species. *Caryologia* 19: 167–196.
- Morgan, W. G., H. Thomas, M. Evans & M. Borrill. 1986. Cytogenetic studies of interspecific hybrids between diploid species of *Festuca*. *Canad. J. Genet. Cytol.* 28: 921–925.
- Nevski, S. A. 1934. *Lolium*. Pp. 545–552 in V. L. Komarov, R. Yu Rozhevits & B. K. Shishkin (editors), *Flora of the U.S.S.R.* Vol. 2. Translation for the National Science Foundation and the Smithsonian Institution, 1965, Israel Program for Scientific Translations.
- Niles, C. D. & A. Chase. 1925. A bibliographic study of Beauvois' *Agrostographie*. *Contr. U.S. Natl. Herb.* 24: i–vi, 135–214, vii–xix.
- Raspail, F. V. 1829. Déviations physiologiques et métamorphoses réelles du *Lolium*. *Ann. Sci. Observ.* 2: 233–244.
- Reveal, J. L., E. E. Terrell, J. H. Wiersema & H. Scholz. 1991. Proposal to reject *Festuca elatior* L. with comments on the typification of *F. pratensis* and *F. arundinacea* (Poaceae). *Taxon* 40: 135–137.
- Saint-Yves, A. 1929. *Festuca* hybrides. *Izv. Glavn. Bot. Sada SSSR.* 28: 592–608.
- Smith, P. 1969. Serological relationships and taxonomy in certain tribes of the Gramineae. *Ann. Bot. (London)* 33: 591–613.
- Soreng, R. J., J. I. Davis & J. J. Doyle. 1990. A phylogenetic analysis of the chloroplast DNA restriction site variation in Poaceae subfam. Pooideae. *Pl. Syst. Evol.* 172: 83–97.
- Stace, C. A. 1975. Hybridization and the flora of the British Isles. Academic Press, London, New York, San Francisco.
- Stebbins, G. L., Jr. 1956. Taxonomy and the evolution of genera, with special reference to the family Gramineae. *Evolution* 10: 235–245.
- Tateoka, T. 1962. Starch grains of endosperm in grass systematics. *Bot. Mag. (Tokyo)* 75: 377–383.
- Terrell, E. E. 1966. Taxonomic implications of genetics in ryegrasses (*Lolium*). *Bot. Rev. (Lancaster)* 32: 138–164.
- . 1968. A taxonomic revision of the genus *Lolium*. *Tech. Bull. U.S.D.A.* 1392: 1–65.
- Thomas, H. M. 1981. The Giemsa C-band karyotypes of six *Lolium* species. *Heredity* 46: 263–267.
- Tutin, T. G. 1956. Generic criteria in flowering plants. *Watsonia* 3: 317–323.
- Tzvelev, N. N. 1989. The system of grasses (Poaceae) and their evolution. *Bot. Rev. (Lancaster)* 55: 141–204.
- Ullmann, W. 1936. Natural and artificial hybridization of grass species and genera. *Herbage Rev.* 4: 105–142.
- Watson, L. & R. B. Knox. 1976. Pollen wall antigens and allergens: Taxonomically ordered variation among grasses. *Ann. Bot. (London)* 40: 399–408.